Observations on the Physiology of Echinodermata. By GEORGE J. ROMANES, LL.D., F.R.S., Sec. Linn. Soc.

[Read March 1, 1883.]

CONTINUING the observations on the nervous system of Echinodermata which some years ago I began in conjunction with my friend Professor J. Cossar Ewart*, and then communicated to the Royal Society, I have thought that, being now Secretary of this Society, it may be more fitting that I should communicate to it the results of my further inquiries.

In the paper already published by the Royal Society, it was shown by experiment that the ocelli situated at the end of the rays in Starfish, and occupying the homologous position in Echini, perform a visual function-inducing the animal to seek the light so long as the ocelli are intact, and the animal ceasing to be affected by light when the ocelli are removed. It therefore occurred to me to try whether these organs of special sense might not have an olfactory as well as a visual function to perform. In order to try this, I procured some fresh starfish. and having placed them on a flat surface covered with shallow water, I dropped little pieces of limpet and crab in their vicinity. None of them, however, approached the food. Knowing that starfish appear to be guided to fishermen's bait by a sense of smell, I thought this result unsatisfactory; and supposing it possible that, having been freshly caught, they might not be in want of food, I left them in a tank for a couple of days, and then repeated the experiment. The result was now quite different, for the starfish began actively to crawl in the direction of the food. Selecting one individual and putting it in a large dish which was filled with sea-water, I found that I could at pleasure lead the starfish in any direction I chose by holding a morsel of crab an inch or two from the end of one of its rays, and continuously withdrawing the food as the starfish continuously approached it. Moreover I could at any time reverse the direction of advance by transferring the food to the opposite side of the animal, and holding it for a short time near the tip of a ray. Thus I could entertain no doubt that starfish have a well-developed sense of smell, which enables

^{*} See the Croonian Lecture, 1881, Philosopical Transactions, pt. iii, 1881, pp. 829–885.

them quickly and accurately to perceive the direction from which the odour of food is coming, provided that the distance of such food as I have named is not more than a few inches from the animal.

With the view of ascertaining whether or not this olfactory sense is localized in the ocelli, I removed the latter from all the rays of the same starfish with the point of a scapel, and then repeated the experiment. The result was the same; thus showing that the ocelli are not specially concerned in the sense of smell. Next I tried the effect of removing the whole tips of the rays; but still there was no change in the result of the experiment. Nor was there any change produced when the rays were progressively truncated further and further down: the olfactory sense was found to be distributed throughout their length.

The question still remained whether this sense was equally distributed on the upper and lower surfaces of the rays. I therefore placed a piece of crab upon the upper surface of the disk of another hungry starfish, and found that the animal carried the food upon its back for any length of time without seeking to remove it with its rays, as starfish seek to remove from that position any source of irritation. I also tried the experiment of varnishing the upper surface of a starfish and placing food before its rays, with the same result as I obtained with unvarnished specimens. It was not practicable-seeing that it would have interfered with the action of the feet-to try the converse experiment of varnishing the under surface while leaving the upper surface unvarnished, or this would have supplied a still better test; but I think that the experiments which were practicable are sufficient to show that the sense of smell is distributed over the lower surface, while not extending to the upper surface.

In all these respects detached rays behave in the same way as the entire animal; but if in the entire animal the central nervering is divided between each of the rays, the animal ceases to follow the food with precision, owing to the loss of coordination between the rays which the operation has entailed.

In the paper already referred to, evidence was adduced to show that, at all events, one function of the pedicellariæ is that of assisting locomotion by seizing fronds of sea-weed, and holding them steady until the pedicels have time to gain attachment by their adhesive disks. Some additional observations tending to strengthen this evidence may here be stated.

If an Echinus is allowed to form its adhesions either by its equa-

torial or its aboral pedicels upon a glass plate placed so as to form the cover of a tank which is filled with water, the Echinus will remain suspended in the water holding on to the glass plate, or ceiling, with as many pedicels as can be brought to bear upon that surface. From the globular shape of the animal, however, only a comparatively small number of pedicels can be thus brought to bear; and an insecurity of anchorage being the result, the Echinus seeks to increase its hold by feeling around for additional supports with its unemployed pedicels. While doing so the pedicellariæ may also be seen to be engaged in a similar quest, and especially those near the surface of attachment; in that vicinity the little forceps are actively swaying about and snapping, as if the animal knew that there was the best chance of encountering pieces of seaweed near the solid surface from which it is depending.

In the Royal Society paper it was stated that when an Echinus is inverted on a flat surface under water, so that it rests upon its aboral pole, it will quickly right itself by using two or more adjacent rows of pedicels. The process is thus described :-- "As many feet upon the adjacent rows as can reach the floor of the tank are protruded downwards, and fastened firmly upon the floor; their combined action serves to tilt the globe slightly over in this direction-the anchoring feet on the other, or opposite, rows meanwhile releasing their hold of the tank-floor to admit of this tilting. The effect of the tilting is to allow the next feet in the active ambulacral rows to touch the floor of the tank, and when they establish their hold they assist in increasing the tilt; then the next feet in the series lay hold, and so on, till the globe slowly but steadily rises upon its equator," after which it descends as slowly into its normal position of resting upon its oral surface. Now these facts led to a discussion of the questions, whether the execution of such a manœuvre was to be considered due to the coordinating influence of a nerve-centre having a dim sense of gravity, and feeling, as it were, this sense disturbed by the unusual position in which the animal is placed; or whether the manœuvre was to be considered due merely to the serial action of the pedicels themselves, such that when the globe is slightly tilted by the combined action, say, of three successive pedicels, A, B, and C, opportunity is afforded for the next in the series, D, E, and F, to reach the floor of the tank, and, fastening upon it, to increase the tilt, so in turn affording an opportunity for the next in the series, G, H, I, to establish

their adhesions, and so on. Such being the questions to determine, sundry experiments were described, with the result of tending to show that the manœuvre must at least in part be due to the coordinating influence of a nerve-centre. Mr. Francis Darwin, having read the account of these experiments, suggested an additional one, which I have tried, with the result of definitely settling the question. This experiment and its results are as follows :—

An Echinus is inverted with its aboral pole resting on the bottom of a large bottle filled to the brim with sea-water. The mouth of the bottle is then corked (no air-bubbles being included), and placed upon the rotating apparatus which Mr. Darwin and his father used for investigating the geometrism of plants. That is to say, the Echinus was continuously rotated in a vertical plane. I found that so long as the rotation was continued, whether rapidly or slowly, the Echinus did not attempt to right itself; but that, when the rotation was allowed to cease, it began to do so after two or three minutes. Moreover, if allowed to do so until it had raised itself into the equatorial, or any other intermediate position, and the rotation were then resumed, the position gained was permanently retained so long as the rotation was continued. Therefore I could entertain no doubt that the effect of the rotation was that of confusing, as it were, the coordinating influence of a nerve-centre, the stimulus to the operation of which, in the absence of rotation, is gravity. As shown in the Royal Society paper, this nerve-centre is in part, though not exclusively, the circumoral ring.

Thinking it might be worth while to try the effect of very rapid rotation upon the coordinating power of this nerve-centre, I tied the bottle containing the Echinus to the spokes of a cartwheel, which was tilted off the ground to admit of free rotation. By means of a long rope coiled round the axle, and then uncoiled as rapidly as possible by my running away with the free end of the rope, the Echinus was submitted to exceedingly rapid rotation for two or three minutes at a time; but I could not see that, on being suddenly brought to rest, the functions of the nerve-centres were in any degree impaired.

As additional proof that the righting movements are due to a sense of gravity leading to coordinating action of the pedicels, I may mention the fact that if an Echinus is inverted in a circular beaker filled with water and of a size just sufficient to contain the animal, so that all the pedicels in all directions are equally in contact with the sides of the vessel, the animal rights itself by rotating in some one definite direction till its oral surface is in apposition with one of the sides of the beaker.

It only remains to give a short account of the effects of nervepoisons on the Echinodermata.

1. Chloroform .- On mixing chloroform with the sea-water containing Echini, the first effect was to stimulate the animals to increased activity-their locomotion becoming more rapid, and their spines being moved about rapidly in all directions. But after a few minutes quiescence began to supervene, and increased till it ended in motionless torpidity-the spines and pedicellariæ being all depressed, and all irritability being suspended. When then removed to a basin containing a large quantity of seawater without chloroform, the pedicellariæ soon began to recover their spontaneity, the stalks becoming erect and mobile, while the forceps resumed their clasping function when stimulated by the introduction of a needle between their mandibles. Next the spines recovered their reflex irritability and then their spontaneity. If the Echinus were inverted when restored to the normal sea-water, it remained inverted for a long time, shifting its position by means of its spines; but eventually it succeeded in righting itself.

2. Caffein.—On first immersion in a saturated solution, the pedicels of Echini exhibited a curling movement, which became progressively more and more languid, while they were at the same time slowly but imperfectly retracted. The pedicels persistently remained partly retracted, while both their spontaneity and irritability, as also those of the spines and pedicellariæ, were almost completely lost. The lantern, however, continued to be faintly responsive to stimulation. On replacing the animals in normal sea-water, they slowly recovered their irritability, and next morning were found perfectly well.

3. Nitrite of Amyl.—The effects, when the nitrite was added to the sea-water, were almost identical with those produced by caffein, except that the pedicels, although motionless, were not curled. On submitting an Echinus, taken out of the water and placed under a bell-jar, to the vapour of the nitrite, the action was more rapid. In both cases recovery became complete upon restoring the animals to normal sea-water.

4. Chloral Hydrate.—A few minutes after exposure to this substance the spines of Echini fall into confusion, and the teeth

of the animals gape widely asunder. Soon afterwards spontaneity and irritability are entirely lost. Prolonged exposure kills.

5. *Alcohol.*—The effects of alcohol are closely similar to those of chloroform, although the torpidity produced is not quite so complete.

6. Strychnia.—On adding some crystals of the sulphate to sea-water the first effect on the Echini was that of making their spines extend rigidly in their radial planes, which gave a striking rosette appearance to the animal. They seemed to be in a state of strain, for though they responded rapidly and strongly to stimulation, they sprang back to their original position so soon as the stimulation was discontinued. On being inverted the animals were unable to right themselves; and on being restored to normal sea-water, the spines retained their rosette arrangement for many hours. On faintly acidulating the water so as to secure a better solution of the alkaloid, the effect on the spines was that of throwing them into great disorder, while all spontaneity and irritability were destroyed. The animals were killed.

7. Nicotin.—A small trace of this substance added to the sea-water is sufficient to determine the speedy death of the Echini exposed to its influence, the spines being thrown into great disorder.

8. Curare (powder rubbed up with a few drops of spirit and distilled water before being added to the sea-water).—The Echini soon became motionless, lost their irritability, but adhered firmly with their pedicels to the floor of the tank, and when forcibly detached again resumed their hold. After a time the animals appeared to be dead, the spines being stiffly depressed but not in disorder. On being transferred to normal sea-water, however, their recovery was rapid and complete.

9. Digitalis.—After exposure for some time to the influence of Digitalis, the Echini lost all their spontaneity and irritability, being therefore to all appearance quite dead; but on being then restored to normal sea-water, they partly recovered. Next day they were found to be moving very languidly, their pedicels not adhering to the tank, and their general irritability being much impaired.

10. Cyanide of Potassium.—For some time after immersion in a very diluted solution of this substance the Echini appeared to

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be none the worse; but suddenly the spines began to become depressed in a disorderly manner, while irritability ceased immediately and entirely. If the dose were not quite strong enough, or the exposure not prolonged enough to cause death, there was nevertheless a permanent weakening of the animals produced; for next day they were found to be but slightly mobile, scarcely at all responsive to stimulation, and not adhering to the tank.

Observations on the Madreporarian Family—the Fungidæ, with especial reference to the Hard Structures. By Prof. P. MARTIN DUNCAN, M.B. Lond., F.R.S., &c.

[Read January 18, 1883.]

(PLATES V.-VI.)

PART I. The History of the Classification of the Fungidæ, and remarks on the Diagnosis.—Remarks on the absence of satisfactory descriptions and delineations of the Synapticula and the resulting confusion.—A description of the Hard parts of *Fungia scutaria* (variety), Lmk., general and microscopical.—Considerations regarding Growth and the Nature of the Interseptal Loculi.

THE family of Aporose Madreporaria called the Fungidæ was established by Dana in 1846 in his Report on the Zoophytes of the Wilkes Exploring Expedition. He defined several genera, and gave beautiful illustrations of the general configuration of species, noticing moreover the tentacular arrangement.

In 1849 MM. Milne-Edwards and Jules Haime published a monograph on the family in the 'Annales des Sciences Naturelles,' sér. 3, tom. xv. ; and, dealing rather with the hard parts than with the soft dermal tissues, they consolidated the knowledge given by Dana, and discovered some new and family peculiarities and deficiencies. They had the advantage of studying large collections of recent and fossil Fungidæ; and they saw the necessity of founding their classification on data derived both from ancient as well as modern species.

In 1860 the great work by these authors, 'L'Histoire naturelle de Coralliaires,' reached the third volume, and the Fungidæ were very carefully described and classified. They differentiated the family, explained most clearly its position in relation to the Aporosa and Perforata, and divided it into subfamilies.

This work has remained, up till lately, the recognized authority